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"Engaging the Enemy": Orangutan (*Pongo pygmaeus morio*) Conservation in Human Modified Environments in the Kinabatangan floodplain of Sabah, Malaysian Borneo

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Abstract

Throughout the equatorial tropics, forest conversion to agriculture often fragments crucial primate habitat. In 30 years, 80% of the alluvial lowland forests along the Kinabatangan River in Sabah, Malaysian Borneo, have been supplanted by oil palm (*Elaeis guineensis*) plantations. Today, only about 20% of the former orangutan (*Pongo pygmaeus morio*) population remains in the region. Because most of the land is now under the tenure of agribusiness companies, we used a pragmatic approach of mixed biosocial methods and citizen science engagement of oil palm growers (N = 6) as active conservation partners to study orangutan use of the privately administered landscape between protected forest fragments. We found that 22 of 25 remanent forest patches (0.5 to 242 hectares) surveyed within plantations contained food or shelter resources useful for orangutans. Of these, 20 are in regular transitory use by wider-ranging adult male orangutans, and in 9 patches, females are resident and raising offspring isolated within oil palm plantations. These findings indicate that orangutans retain a measure of normal metapopulation dynamics necessary for viability at the landscape level despite drastic habitat modification. We found that barriers to in situ conservation in these agroforest matrices were due to the following misconceptions across sectors: 1) Good farming practices require exclusion of wildlife; 2) Orangutans seen in plantations must be "rescued" by people; and 3) Translocation is an appropriate conservation strategy, and nondetrimental to orangutans. Our exploratory study exemplifies the value of biosocial methods and collaboration with industrial-scale farmers to support primate resilience in forests fragmented by agriculture.

Keywords Orangutan · Oil palm · Agro-forestry · Fragmented habitat · Anthropogenic landscapes · Biosocial methods

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Introduction

With few exceptions, the world's nonhuman primates are native to the equatorial tropics (Bourliere, 1985; Van Schaik & Pfannes, 2005). Over the past 50 years, this region has experienced rapid land-use change, mainly driven by agricultural expansion (Houghton & Nassikas, 2017; Lambin et al., 2003; Ramankutty et al., 2002). Madagascar, South, and South-East Asia are most affected, while forest conversion to agriculture is increasing across the equatorial belt in Africa, Central America, and tropical South America (Almeida-Rocha et al., 2017). As a consequence of human-mediated land use change, nonhuman primates (hereafter primates) suffer habitat loss and displacement (Estrada et al., 2017). Primates often can withstand a degree of habitat degradation from selective timber extraction and some fragmentation from agricultural conversion if partitioned forests are not so isolated from each other that access between them becomes impossible (Ancrenaz et al., 2010; Marsh, 2003; Marsh & Chapman, 2013). However, excluding wildlife from farms is a central dogma of agricultural practice and sequestering wildlife within designated protected forests is common to most animal management policies (Lele et al., 2010; Pascual et al., 2021). These restrictions on the movement of wildlife and people further challenge primate resilience in agroforestry landscapes (Andayani et al., 1998; Hill, 2005; Hockings & Humle, 2009; Sherman et al., 2020a; Treves et al., 2006). Therefore, even the most ecologically flexible primates suffer reduced resources and dispersal opportunities with progressive habitat loss (Reynolds et al., 2003; Afendi et al., 2011; Ménard et al., 2014; Donati et al., 2016; Bicca-Marques et al., 2020). Other factors tangential to agricultural land-use change, such as new road construction and the expansion of human settlements, with their concomitant risks of poaching, accidents, and potential exposure to new diseases, increase the obstacles to primate survival in anthropogenic landscapes (Azhar et al., 2013; Clements et al., 2014; Bublitz et al., 2015; Almeida-Rocha et al., 2017; Sloan et al., 2018; Garriga et al., 2019; Gould & Cowen, 2020; Boonratana, 2020).

Commensurate with habitat shrinkage and fragmentation, wildlife often are forced into closer proximity with humans, increasing the chances for people–primate encounters (Humle & Hill, 2016). Direct costs to people resulting from interactions with primates include crop loss, property damage, and attacks that can result in injury, illness, and even death (Hill & Wallace, 2012). Direct costs for primates are similar: loss of natural food sources by displacement with crops intended for human consumption, conflict over crop foraging, loss of free access across the landscape, injury, illness, and even death due to being attacked or killed by people (Campbell-Smith et al., 2012; Hockings & Humle, 2009; McLennan et al., 2012; Meijaard et al., 2011). Primates also face an increased risk of loss by live capture and transfer to captive care via the pet trade in anthropogenic environments (Freund et al., 2017). Individuals confiscated from exploitation often require costly and labour-intensive rehabilitation to readapt to life in the wild, which may dilute resources and foster misunderstanding about the importance of conservation of already competent wild populations (Palmer, 2018; Wilson et al., 2014). The chief indirect costs of proximity for both people and wildlife are mutual fear that can induce stress and misconceptions that result in mitigations that may alter but not fully resolve conflict (Campbell-Smith et al., 2012; Davis et al., 2013; Hill, 2004; Hill & Webber, 2010; Marchal & Hill, 2009; McLennan & Hill, 2012).

Over the past 40 years, wide-scale forest conversion for growing oil palm (*Elaeis guineensis*) on the islands of Sumatra and Borneo overlaps with the remaining range of the orangutan (*Pongo* spp.), an iconic species with worldwide appeal (Koh & Wilcove, 2008; Gunarso et al., 2013). Orangutans are the largest habitually tree-living mammal and require diverse native forests, especially in alluvial mosaic habitats where they historically exist at the highest densities (Cant, 1980; Marshall, Ancrenaz, et al., 2009; Rijksen & Meijaard, 1999; van Schaik et al., 1995). These fertile areas also are most favoured for agriculture (Abram et al., 2014; Gaveau et al., 2014).

During land conversion operations on Borneo and Sumatra, orangutans often are killed or removed live and translocated by hard release to other forested areas (Kilbourn et al., 2003; Wich et al., 2016; Sherman et al., 2020a, b). Government agencies or contracted NGOs usually conduct these wild-to-wild translocations, and relevant skills or resources are rarely available for post-release monitoring (Sherman et al., 2020b). Adult male orangutans, being the dispersing sex, tend to move away from habitat disturbance if possible (Ancrenaz et al., 2010; Haile, 1963; Nietlisbach et al., 2012). In contrast, the philopatric nature of adult females and immatures tends to compel them to remain in place even in cases of drastic habitat loss (Arora et al., 2010; Ashbury et al., 2020; Felton et al., 2003; Goossens, Setchell, et al., 2006; van Noordwijk et al., 2012). Those animals of either sex that escape initial wildlife clearance operations often subsequently face starvation due to a rapid decline in forest-contingent resources or are killed or translocated for foraging on first planting seedlings (Nellemann, 2007; Wich et al., 2012; Hardus et al., 2012; Ancrenaz et al., 2015; Wich et al., 2016).

The rate of forest loss is unabated in Indonesian Borneo (Kalimantan) but has slowed in Sumatra and Malaysian Borneo, mainly due to a lack of large tracts of land suitable for industrial-scale oil palm plantation development (Santika et al., 2017; Xu et al., 2020; Yunikartika, 2016). Furthermore, land conversion for other uses (e.g., mining, dam construction, and road building, including the Pan Borneo Highway) is ongoing throughout the orangutan's range, including the imminent threat to the newly described Tapanuli species (*Pongo tapanuliensis*) in Sumatra (Alamgir et al., 2019; Laurance et al., 2020; Wich et al., 2019). Thus, habitat insecurity from encroachment and further fragmentation is an ongoing and central concern for wild orangutan conservation (Wich et al., 2016; Gaveau et al., 2019; Voigt et al., 2021).

Despite being large-bodied, orangutans are highly cryptic, so direct encounters are rare, especially by people unfamiliar with orangutan behaviour. Moreover, orangutans maintain a more diffuse fission–fusion sociality than other great apes and, being generally solitary foragers, are customarily distributed at low densities over broad areas (van Schaik, 1999). These traits led to the presumption that orangutans could only survive in extensive intact forests (MacKinnon, 1971; Rao & van Schaik, 1997). However, most orangutans now dwell within forests degraded by some degree of timber extraction on Sumatra and Borneo (> 80% of all orangutans in Sabah and > 75% in Kalimantan—SWD, 2020; Ancrenaz et al., 2016; Wich et al., 2016).

Fortunately, orangutans survive in degraded and fragmented forests, particularly in places without extensive silviculture forest management and where hunting orangutans is not traditionally practised (Lackman-Ancrenaz et al., 2001; Ancrenaz, Calaque, et al., 2004; Marshall et al., 2006; Campbell-Smith et al., 2011; Oram, 2018). Systematic ground, aerial helicopter and drone surveys also have reported signs of orangutans in mixed agro-forest landscapes (Meijaard et al., 2010; Ancrenaz et al., 2015; Spehar & Rayadin, 2017; Seaman et al., 2021; Milne et al., 2021; Ancrenaz et al., 2021). Therefore, when conditions are favourable, orangutans appear to be more resilient than previously thought. Nevertheless, given their exceptionally long and slow development (mean maternal age at first birth, 14.6 years) and long interbirth interval (mean 7.6 years), wild orangutan populations are particularly susceptible to catastrophic population crashes (Goossens, Chikhi, et al., 2006; van Noordwijk et al., 2018). Furthermore, the polarisation of the debate opposing orangutan conservation and oil palm development leads to misperceptions, suspicion, scepticism and friction between primatologists, industries, governmental and non-governmental conservation agencies, communities, and consumers across the world (Nellemann, 2007; Meijaard et al., 2012; Meijaard & Sheil, 2019; Teng et al., 2020). This situation makes multistakeholder engagement in anthropogenic landscapes critically important and considerably challenging (Nantha & Tisdell, 2009; Spehar et al., 2018).

We used mixed biosocial methods and citizen science engagement with oil palm growers to study orangutan use of the privately administered landscape between protected forest fragments in the Kinabatangan River floodplain of Eastern Sabah, Malaysian Borneo. Our first objective was a field survey to assess orangutan use and habitat quality of remnant forest patches within oil palm plantations. Our second objective was to collect orangutan sighting reports and characterise the observations and viewpoints of local oil palm estate managers and field staff on large scale plantations through formal and informal interviews. From these ground-level engagements, our goal was to initiate ongoing citizen science reporting partnerships with local estates to facilitate landscape-wide conservation of the remaining wild orangutan population in the Kinabatangan region while providing insights relevant to support orangutan survival in forests fragmented by oil palm agriculture throughout their remaining range on Borneo and Sumatra.

Methods

Study region

Within the 500,000 ha Kinabatangan floodplain region, 85–90% of the land is now a mature oil palm landscape interspersed by 41,103 ha of fully protected but largely disconnected forest fragments ranging in size from 100–7,330 ha (Sabah Forestry Department, 2020) (Fig. 1). Selective commercial-scale timber extraction in the region began in the early 1950s (Ibbotson, 2014). Subsequently, outright forest loss by conversion to oil palm monoculture increased exponentially from the mid-1980s (McMorrow & Talip, 2001) (Table 1). In August 2005, the state formally sequestered

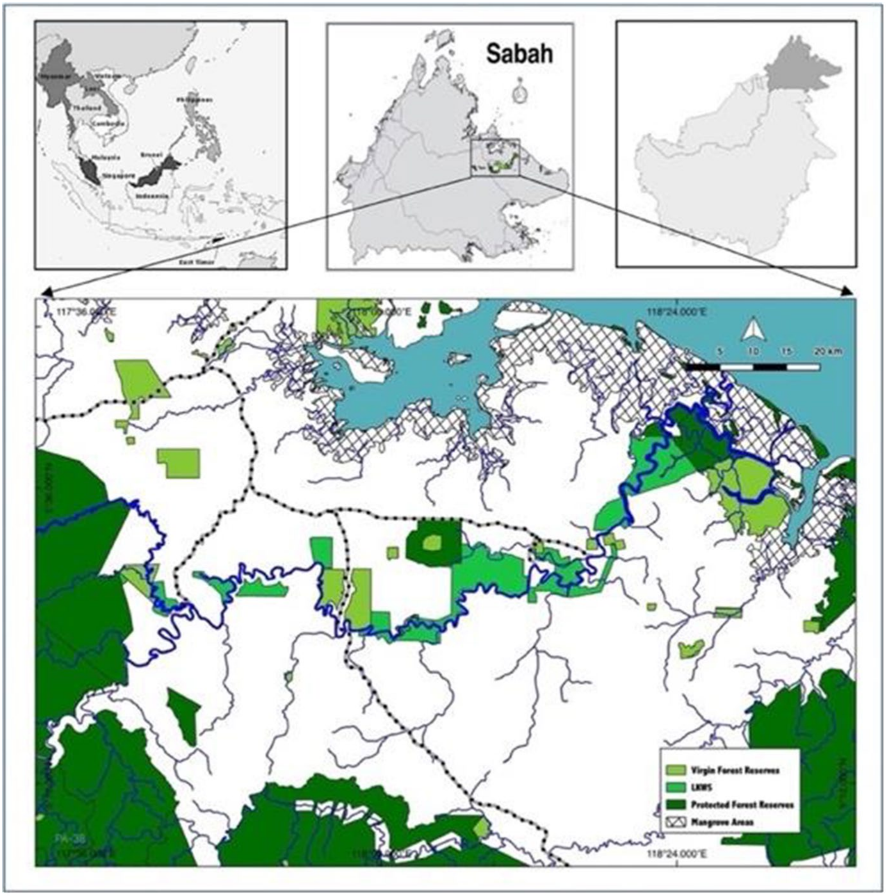

Fig. 1 The 500,000 ha Kinabatangan engagement region in 2020, in Sabah, Malaysia. White denotes privately administered oil palm plantation land. A dashed line indicates main sealed roads, and solid lines are rivers and streams. All solid filled areas are forests with varying degrees of protected status: totally protected virgin forest reserves and wildlife sanctuary, and Forestry Stewardship Council (FSC) certified sustainable native species production forests. Cross-hatched areas are mangrove forest reserves, protected against habitat disturbance and hunting, but fishing is allowed

26,103 ha of remaining degraded forest fragments fronting the Kinabatangan River into a new protected, albeit discontinuous, network. The state acquisition almost tripled the preexisting local protected land formerly consisting of 15,000 ha of intact Virgin Jungle Reserves (VJR). These protected forest fragments are now collectively referred to as the Lower Kinabatangan Wildlife Sanctuary (LKWS) (Ancrenaz, Goossens, et al., 2004) (Fig. 1). The marked increase in protected forest area reduced the amount of land available for agricultural conversion, so new oil palm plantation development decreased sharply from 2006 (Table 1). Since 2010, forest loss for oil palm agriculture has tapered off even further, but conversion continues when new land can be acquired (Gunarso et al., 2013).

Table 1 Kinabatangan orangutan population and rate of forest loss over time 1980–2012, Sabah, Malaysia

Year	Orangutan population numbers	Decline	Rate of regional forest loss to oil palm agriculture	Reference
1980	4000			Payne & Davies, 1982
1990—2000			10% annual increase in land under oil palm cultivation	Gunarso et al., 2013
2001	1,125 95% CI, 691–1,807			Nest transect survey Ancrenaz, Goossens, et al., 2004
2006	815 95% CI, 426 -1,418	2001–2006 6.2% per annum		Nest transect survey SWD, 2012
2006—2010			2.2.% annual increase in land under oil palm cultivation	Gunarso, et al., 2013
2015	785 95% CI, 425—1,467	2006–2015 0.42% per annum		Nest transect survey Ancrenaz et al., 2016

Local orangutan population

The focal species of this study is the northeastern subspecies of the Bornean orangutan (*Pongo pygmaeus morio*). Sabah is home to the largest remaining numbers of this subspecies (Ancrenaz et al., 2016). Quantitative orangutan counts by nest surveys in 1999, 2006, and 2015 revealed an ongoing population decline, albeit at a reduced rate following gazettement of the LKWS in 2005 (Table 1). A good reservoir of long-term eco-ethological knowledge of wild orangutans exists in the Kinabatangan region from the continuous study by the HUTAN Kinabatangan Orangutan Conservation Programme (KOCP) since 1998.

Definition of key terms

We defined "forest patches" as areas with a minimum size of 0.5 ha where some nonoil palm vegetation remains within monoculture cropland. Oil palm companies commonly refer to these forest patches as "unplantable areas." Many patches were on steep and rocky terrain on hills and in ravines. Flatter water catchment areas were usually left relatively undisturbed. In the mature oil palm landscape of the Kinabatangan region, we found that "unplantable areas" often were devoid of commercial timber species but otherwise were native species forests in natural recovery with no restorative forest management (i.e., silviculture, enrichment planting, or invasive species control) for the past 10–40 years. Estates often use more accessible "unplantable" areas as quarry sites for road building materials, for physical training, or recreational use by plantation staff and occasionally for nonoil palm agriculture. Monoculture oil palm surrounds most forest islands on privately administered land.

This study focused on engaging oil palm growers with extensive holdings (8,500–75,000 ha) in the Kinabatangan landscape. "Estates" are the smaller management units of large plantation company holdings, usually between 1,500 and 3,000 ha in size. We discovered during this study that many forest patches were in boundary areas between different company's holdings, and ownership was not always clear. Therefore, we did not target specific forest patches in the initial study design. Instead, we engaged with interested companies first and then were directed to "unplantable areas" by estate managers when we arrived on site.

Survey of small forests in oil palm monoculture and citizen science engagement of estate staff

We conducted exploratory survey work in 2019 and 2020 to identify remanent small forest patches within oil palm plantations, rapidly assess habitat value to orangutans, and establish the presence/absence of signs of orangutan use. Because we were working on privately administered oil palm agricultural land, engagement, and involvement of company staff, as the key stakeholders, was central to the study process. Equally important was to initiate collaborative citizen science participation and monitoring towards the longer-term goal of integrative conservation of wild orangutans across the private/protected forest landscape

(Ancrenaz et al., 2015; Setchell et al., 2017; Waters et al., 2019). One to four estate staff always accompanied us on our on-site work for transparency, partnership development, and mutual capacity building. On initial site visits, up to 30 other company representatives, including regional sustainability managers, often joined us as well. Survey duration varied with forest patch size, but we initially spent 1 to 4 days on each site. We also collected orangutan sighting reports from estate records and conducted interviews with field labourers and supervisors who work in the areas around forest patches.

The same skilled orangutan researcher team familiar with the local Kinabatangan landscape led all survey work. Each team member involved in these studies had 10 to 25 years of experience locating, habituating, and conducting individual focal-follow behavioural studies of wild orangutans (Lackman-Ancrenaz et al., 2001; Oram, 2018). Given the vulnerability of orangutans on privately administered land, it was not prudent to actively pursue habituation for focal follows at this early stage of engagement. However, we did use our experience to reliably identify specific individuals by opportunistic neutral contact (Williamson & Feistner, 2003). The mean height of trees in degraded forests in the Kinabatangan region is 17 m, with few trees above 30 m, which helped us recognise animals (Ancrenaz, Calaque, et al., 2004; Davies et al., 2017). We trained in visual body scoring and general health assessment via our association with the Orangutan Veterinary Advisory Group (OVAG) network (Clingerman & Summers, 2005; Pramesywari, 2013; Reamer et al., 2020).

Once we synthesised the initial survey information with data acquired from oil palm staff records and field interviews, we followed up on the ground with monthly site visits when possible, especially in areas of recent and routine orangutan use. We also set up a series of small closed text message groups to maintain ongoing, communication by forest patch or estate. Using the mobile telephone application "WhatsApp," the research team and relevant oil palm grower staff systematically collected and shared monitoring data, addressed questions, and mitigated conflicts together. We ensured all participants recognised the need to maintain the integrity of the information relayed in these closed groups to not place any orangutans at any additional risk by tracking their movement.

Disturbing wildlife refuge areas by extensive cutting of dense undergrowth or rigging climbing equipment to manage steep slopes safely would not support conservation in these small forest patches. Therefore, we used preexisting dirt roads or pathways that usually ringed each forest patch to conduct reconnaissance walks by circumnavigating the perimeter on foot or in a slow-moving vehicle with periodic stops (Kühl et al., 2008). If it enhanced our ability to survey systematically, we also traversed the patch on preexisting paths where possible. Using good vantage points and binoculars, one to three experienced project field researchers conducted these surveys, assisted by two to four estate sustainability staff. We took great care to view as much of the whole patch as possible in each case. We quantified orangutan use during these reconnaissance surveys by cataloguing feeding signs, evaluating sleeping nests built daily by orangutans locally, recording occasional opportunistic animal sightings, and assessing habitat quality by an index scale (Ancrenaz, Calaque, et al., 2004: Kühl et al., 2008).

We did not establish a minimum threshold count of nests or signs. However, we did note the pattern, distribution, and relative age of nests and feeding signs to establish broad patterns of temporal use (Table 2). We also used a standardised index scale to measure nest class as an indication of time since construction as follows: 1 = new: all green leaves; 2 = recent: all leaves dry and brown; 3 = old: some leaves are gone but nest shape and structure still well defined; 4 = very old: holes visible in nest; 5 = almost gone: a few branches and twigs, indicating presence but otherwise structure no longer discernible (Ancrenaz, Calaque, et al., 2004). Pioneer tree species *Neolamarckia cadamba* (Laran) and *Pterospermum* spp. (Bayur), the second and fourth most selected by orangutans for nests locally, are common in these small forest patches on estates (Oram, 2018). These two tree species also have a mean decay rate consistently near the overall local mean of 202 days (Ancrenaz, Calaque, et al., 2004). Therefore, these trees were helpful for decay rate comparisons within and between patches.

For habitat quality measurement (Table 3), we noted plant species in the top 20 most consumed species by orangutans in 2010–2016 in the HUTAN study site, especially those that provide food regularly and supply good cover and shelter as nest sites (Oram, 2018). Those patches with at least 2 of the top 5, one third of the top 20 food species overall, and nest species trees at least 20-m tall received a "very good" ranking. Some key vine species important for orangutans locally are *Spatholobus* spp., *Lophopyxis maingii*, *Gnetum gnemoides*, *Bauhinia borneensis*, and *Bridelia stipularis*. Some key tree species are *Neolamarckia cadamba*, *Dracontomelon* spp., *Diospyros* spp., *Ficus* spp. *Eugenia* spp, and *Xanthophllium* spp. *Nauclea* spp. (Oram et al., in prep). We used Spearman rank

Table 2 Index scale definitions to quantify temporal use of forest patches by orangutans in the Kinabatangan region, Sabah, Malaysia, for surveys 2019–2020

Use	Definition
Recent (within the past month)	Established by the presence of Class 1 nests indicating they were built within the past month and/or fresh orangutan feeding sign, i.e., fruit peels, spat or dropped seeds or freshly stripped bark and the discarded cambium fibres on the ground after orangutans have extracted the plant sugars if these food resources were available in the forest patch
Routine (ongoing residential use or frequent transitory use)	Established by the presence of a continuum of ALL nest classes (1–5) and signs that the tallest most suitable nest trees had characteristic "scars" of past orangutan nests, i.e., trees with broken crowns, presence of regrowth of "greensick breaks" on branches characteristic of orangutan nest building techniques (Davies et al., 2019; van Casteren et al., 2012)
Intermittent (only periodic and transitory use)	Established by the presence of nests only in discrete class groups indicating a break in time when the patch was not used. For example, if we found ONLY Class 3 and Class 5 nests in trees with similar decay rates, there was a gap in time when no orangutan built a nest in the area

Table 3 Index of habitat quality for orangutans to describe forest patches in oil palm plantations in the Kinabatangan region, Sabah, Malaysia, for surveys in 2019–2020

Index value	Description
Poor	Few if any trees, native or otherwise, above 8 m, little to no cover for hiding, covered by grass, or dominated by nonnative invasive species of no use for orangutans as food resources.
Adequate	Low overall value or value is highly nonuniform throughout the patch, i.e., some cover but also routinely used by people. These patches may be generally useful as a short-term rest stop or possibly a low-value feeding stop on a regular basis or may contain a higher quality but highly seasonal feeding species. The patch must at least contain a few natural species trees of at least 15-m tall suitable for nesting.
Good	Forest patch is uniformly useful for orangutans. Covered with trees with at least a third 15 m in height. More and better cover for hiding than “Adequate.” If there is sign of human use, it is minimal and intermittent. Reliable but limited diversity of food resources, especially pioneer species (i.e., *Neolamarckia cadamba*) valuable both as nest sites and food resources but not necessarily any high value seasonal fruit species trees. Presence of key vine species that add cover and provide less clumped food resources.
Very Good	Better overall forest structure and more diversity and richness of native species than “Good.” Multilevel forest structure throughout the patch. Native trees are at least 20-m tall, over a third of the patch. Good natural vine cover. Discrete areas of more secluded habitat that are difficult for people to access, i.e., ravines. Plant species diversity is sufficient to provide reliable food and various plant parts necessary for a balanced orangutan diet (i.e., fruit, leaves, flowers, cambium). Minimal to no use by people. Minimal or well sequestered nonnative invasive species.
Excellent	More areas where access by people is extremely difficult, i.e., very steep ravines with thick natural vine profusion and richer, more diverse native species for greater reliability and balance of food resources than “Very Good.” Less invasive plant species encroachment and restricted human use that is sign boarded as such. “Excellent” patches are either intact, with little sign of past timber extraction or in natural recovery for an extended period (30–40 years). Commercially exploited timber species are not primary food sources for orangutans in the Kinabatangan region, so selectively logged forests are not necessarily inadequate for this species (Ancrenaz et al., 2010; Ancrenaz, Calaque, et al., 2004; Ancrenaz, Goossens, et al., 2004; Lackman-Ancrenaz et al., 2001; Oram, 2018).

correlation tests (cor.test function in R version 4.0.4 (2021–02-15) for bivariate analysis to measure the strength of association between habitat quality and patch size and habitat quality and those forest patches used by orangutans.

We gauged the level of use by people during interviews with managers to learn estate policy and through follow-up questions with field labourers who live or work near small forest patches on estates. We factored proximity to human habitation into the habitat quality assessment. We also noted signs of human use (i.e., presence of picnic areas, sheltering structures, litter, signs of extractive use by people, equipment, such as ropes to descend steep slopes), and direct sightings of people using the area.

Field staff interviews

As a precursor to field engagement in 2019–2020, we conducted a series of structured interviews in 2012 and 2013 to establish if oil palm field labourers on 9 Kinabatangan oil palm estates encountered orangutans in the course of their work and, if so, to catalogue their experience. These interviews formed the baseline for subsequent survey work and citizen science engagement. Almost all oil palm field labourers in Sabah are foreign workers on restricted access contracts and live full-time on their work estates. These labourers are most often from rural areas in isolated parts of Indonesia or the Philippines and are generally unfamiliar with being asked questions by people other than their employers. Most managers of large estates are from other parts of Sabah or peninsular Malaysia. Therefore, it was essential to establish trust from both an efficacy and ethics perspective. To this aim, local team members of the community conservation NGO, HUTAN-KOCP, who are native to the Kinabatangan region and familiar with the broad range of people living in the area conducted initial interviews in 2012 and 2013. We workshopped all aspects of this initial engagement, including how to contact and coordinate with estates and structure questions, with the same team to achieve proper phrasing, so that questions were not off-putting to interviewees, and interviewers could ask potentially sensitive questions in a way that was comfortable to them. We wrote questions in simple conversational Malay, but used Indonesian, Suluk, and English during interviews when necessary. Interviewers used a series of photographs of all age-sex-class combinations of orangutans and monkey species to help identify animals encountered. Local specialist orangutan field researchers were present to help evaluate sighting reports. We held all interviews one-to-one, out of earshot of fellow respondents. Interviewers wrote down the answers and read them back to the interviewee to assure accuracy. We did not record conversations, primarily because, when we suggested this, managers and workers were more hesitant to participate and more suspicious of our intent because they felt someone could potentially manipulate a recording of their voice through editing. We found that the extra time to interview without recording was beneficial because it yielded valuable additional volunteered information and created a foundation of cooperative goodwill. We conducted pilot interviews with 23 oil palm field workers from smaller plantations not involved in the more extensive study.

Ethical note

The Sabah Government Departments of Wildlife and Forestry approved this work. Although the project was funded in part by the independently administered charitable foundation (Yayasan Sime Darby) of a multi-faceted Malaysian company that includes an oil palm industry division, there was no oversight by or obligation to the parent company for work done by this project. We conducted this study without any commercial or financial relationships that could be construed as a potential conflict of interest.

Data Availability

Despite being fully protected, orangutans in this landscape are not safe from unnatural loss. Therefore, the datasets generated during this study are not publicly available to protect the orangutans in this anthropogenic landscape and to respect the privacy of some collaborating oil palm companies. Some further details may be available from the corresponding author on reasonable request. We reported a broad general overview of a larger dataset of initial interview results from 2012 and 2013 that included smallholder oil palm plantations ≤ 10 ha in Ancrenaz et al. (2015). Details reported here were not included in the previously published material.

Results

In 2019 and 2020, we surveyed 62,437 ha of oil palm plantation land, covering approximately 12.5% of the overall 500,000 ha Kinabatangan region. We located 25 nonoil palm planted forest patches, from 0.5 to 242 ha (median 13.5 ha), within 23 oil palm plantation estates owned by 6 companies. We found all 25 forest patches were 10 km or less from another forest or mangrove area on the same side of the Kinabatangan River, and in 18 cases (72%), the nearby forest had protected status. Furthermore, we found that 23 of 25 (93%) were 5 km, and 17 of 25 (68%) patches were ≤ 2 km from another forest refuge. All forest patches were surrounded by oil palm except one 50-ha patch that adjoined a 1,500-ha protected forest reserve. Additionally, 15 of the 25 patches within estates were on hills, providing good vantage points to view other forest "stepping-stones" across the landscape.

Habitat quality value for orangutans of small forest patches on oil palm estates

The modal habitat quality for all 25 patches surveyed was "good" (range "poor" – "excellent"). We found that orangutans used patches (N = 20) with a habitat range from "adequate" to "excellent" with a mode value of "good" (Table 4). The habitat quality mode for patches that contained resident orangutans was "very good," with a range from "good" to "excellent" (N = 9 note: 10 adult females live in 9 forest patches). Only 2 (8%) of the 25 forest patches were relatively intact, i.e., still contained mature stands of commercial timber species, e.g., *Dipterocarpus* spp. Both of these two patches had a habitat quality ranking of "excellent." All others (N = 23, 92%) showed signs of degradation from varying amounts of commercially important native tree species extraction, usually when initial forest clearing occurred 10–40 years ago. Habitat quality rankings of degraded forest patches

Table 4 Habitat quality ranking of forest patches surveyed in oil palm plantations in the Kinabatangan region, Sabah, Malaysia, 2019–2020 (see Table 2 for habitat quality index definitions)

Orangutan Habitat Index Ranking	Unused by orangutans (N = 5)	Used by orangutans (N = 20)
Poor	2	0
Adequate	1	6
Good	2	5
Very good	0	4
Excellent	0	5

(N = 23) ranged from "poor" to "excellent". Although orangutans do not rely exclusively on terrestrial water sources, we found streams or small rivers were common to all patches that received an orangutan habitat index score of "very good" and "excellent."

Two of the five forest patches with no sign of orangutan use had a "good" habitat quality ranking. Despite favourable tree architecture, there was no evidence of broken or misshaped tree crowns indicating use as a nest site in these two patches even in the more distant past (1–5 years) (Ancrenaz, Calaque, et al., 2004; Davies et al., 2019). The larger patch (27 ha) was 10 km from another forested area, but only in one direction. It was 20–30 km from other forests in all other directions and was 1.7 km from the intersection of two major sealed roads. The smaller unused patch (4 ha) was less than 2 km from a mangrove reserve. However, this forest patch was 800 m from a plantation "village" (grouped field staff accommodation) and routinely used by people. In one other case, worker housing was adjacent to a patch with a resident female, but forest patch use by staff was prohibited.

Another forest patch unused by orangutans was a stand of non-native teak, *Tectona grandis* (local name: Jati), between 15–20 m tall, planted about 20 years ago. Based on the secluded location, overall proximity to other forests, tree height, stability, and architecture orangutans generally select for nesting, we expected that this patch, although lacking in food resources, might at least be suitable as a nest site for migratory males (Cheyne et al., 2013; Davies et al., 2017). Hence, we gave it a habitat index ranking of "adequate." However, we found no sign of orangutan use of this stand of exotic timber species. Two other unused patches received a habitat quality score of "poor." These were both wholly overrun by invasive *Mucuna bracteate* vines at least 1-m deep, covering all surfaces, including the very few mature trees present. Estates plant this fast-growing vine species as a cover crop to enrich soil nitrogen, prevent weed growth, and control soil erosion in oil palm stands. These vines readily spread into forest patches, choke preexisting natural vegetation, and inhibit native species recruitment. We found encroachment by *Mucuna bracteate* in 16 of 25 (64%) forest patches surveyed. We have not observed orangutans eating this non-native species, and its highly tangled nature makes access challenging even for orangutans. However, we have observed maroon langurs, *Presbytis rubicunda*, feeding on this vine.

Orangutan use of forest islands in oil palm estates

Most small forest patches within oil palm estates used by orangutans (N = 20) contained signs of use within the past month of the survey: "recent" (N = 19) (Table 5). Most (N = 16) also had signs they were used "routinely" either on a frequent transitory basis or by resident individuals. The difference between resident and routine–transitory use was sometimes straightforward to distinguish if food resources were very limited or only highly seasonal, or if the patch was small enough and open enough to be readily traversed and searched by experienced field researchers.

From a synthesis of survey findings, vetted sighting reports, interviews of oil palm labourers who work adjacent to forest patches, and follow-up work on the

Table 5 Details of orangutan use of small forest patches in oil palm plantations in the Kinabatangan region, Sabah, Malaysia, from surveys in 2019–2020

Orangutan use parameters	Ratio of patches with sign listed at left to total patches with orangutan sign (%)
Recent use (within past month of survey)	19/20 (95)
Routine use (repeated residential use or frequent transitory use)	16/20 (80)
Intermittent or periodic use	4/20 (20)
Feeding sign—Presence of characteristic fruit, cambium or termite feeding sign. Consumption of leaves, young shoots, flowers, and insects uncontained in a nested structure (i.e., ants) are usually not readily detectable as a feeding sign. Therefore, the presence of "no feeding" sign does not mean that no feeding took place	11/20 (55)
Orangutan encounters in patches by project research staff	3/20 (15)
Orangutan encounters in patches by estate staff, vetted by research staff	14/20 (70)
Residential use by orangutan female(s) indicated	9/20 (45)
Residential use by orangutan female(s) with dependent offspring confirmed	5/20 (25)

ground, we found that 10 adult females likely are residents in 9 unprotected forest patches within 62,437 ha of oil palm plantation land surveyed. These females appeared to use forests within surveyed estates that ranged from 17–242 ha (median 52 ha). However, we may have underestimated the total forest resources available to these females. We generally did not have access to neighbouring estates to see if they may use more natural forest resources possibly available across a company border. In 5 of the 10 cases, we have visual confirmation of these females. All of these had dependent offspring. The adults had body scores ranging from 2.5 "lean" to 3.0 "optimum" (Clingerman & Summers, 2005). All dependent offspring (0–7 years old) appeared in good condition with an "optimum" or 3.0 body score. In two cases, an older adolescent (8–14 years) accompanied the female and baby. These adolescents had body scores of 3.0 and 3.5 (slightly overweight),

We found a small positive association between habitat quality and patch size, but this was not statistically significant (Spearman's rank correlation: $r_s(18)=0.386$, $p=0.057$, $N=20$). However, we found a significant positive correlation between habitat quality and orangutan use of a patch ($r_s(18)=0.510$, $p<0.01$, $N=20$) and a highly significant and stronger positive association between habitat quality and residential orangutan use ($r_s(7)=0.738$, $p<0.0001$, $N=9$; 2 females live in 1 patch of 236 ha, so 10 females live in 9 patches).

Interviews with field worker staff and management

In 2012 and 2013, we conducted initial interviews with 487 oil palm field labourers in the Kinabatangan region. Respondents represented 13–23% of the general field labour staff on 9 mid-size to larger estates (mean size—2800 ha, range 1,500–4,200 ha). Though 34% (N = 167) of the respondents claimed to have seen an orangutan, only 23% (N = 113) could correctly identify an orangutan in a series of photographs, and only 19% (N = 91) reported an encounter with an adult orangutan in the Kinabatangan region within the past 5 years (N = 99). No unaccompanied immature orangutan encounters were reported during formal interviews in 2012 and 2013. Of the 99 adult orangutan encounters, 83% (N = 82) were made by labourers who work alone, or at most in pairs, for extended periods in the oil palm stands. Female orangutans (N = 18) and immatures (N = 17) were only encountered on forest oil palm borders less than or equal to 10 m from the forest. However, oil palm labourers reported encounters with male orangutans throughout contiguous oil palm ≥ 5 km from a forested area (N = 35) and ≤ 20 m from a forest/oil palm border (N = 33) (Table 6).

Most respondents reacted neutrally to an orangutan encounter (Table 7). Conversely, most workers described the orangutan's response to being detected as negative. Workers generally interpreted the orangutan's actions as being "angry." However, the orangutan's use of distress vocalisations, breaking branches, sudden rapid movements to shake leaves, and branches are expressions of fear and distress rather than aggression based on the authors' long-term experience with the species. Orangutans also were perceived to be "arrogant" by some (N = 26), because they just passively continued what they were doing (N = 12) or did not readily run away (N = 24). Consistent with general estate practice for managing macaques (*Macaca fascicularis* and *Macaca nemestrina*), the most commonly encountered primates in oil palm estates, workers reported they attempted to get orangutans to leave an area by waving their arms, running at them on foot or near them in a vehicle, making noise, and throwing objects, including firecrackers. However, two respondents mentioned it was more effective and expedient with orangutans to just back away and give these animals space, as they would readily leave the area if left alone.

No worker or manager from 2012–2020 reported that losses from orangutans foraging on oil palm fruits were a problem. All oil palm staff from 2012–2020 said orangutans pull up newly planted oil palm seedlings in recently converted areas; however, only one respondent in our formal interviews in 2012, 2013 (N = 487) reported they had observed an orangutan doing this. The three reports of orangutans in subsistence fruit trees or gardens adjacent to employer provided housing within estates were the only incidents where respondents had an explicit negative view of the animals' action. This was because they planned to eat this fruit themselves. However, in all cases, they also expressed they did not view the orangutan itself negatively, recognising "it was just trying to survive."

Standard practice on all estates that we engaged with in the Kinabatangan region was for managers to report sightings to government wildlife authorities when the orangutan appeared "unwell," was out of sight of a protected forest border and therefore considered "lost," or appeared to stay in one place on the estate despite efforts of staff to encourage it to "move away". The expectation of the oil palm companies and the subsequent action by wildlife officers was to try to capture the orangutan, remove it from the plantation, administer veterinary care if needed and then translocate healthy animals to a larger protected forest area, preferably in a different region, so the animal would be unlikely to return again to the same area.

Table 6 Summary of orangutan sightings (N = 99 adults, excluding immature dependent offspring) reported by 91 oil palm field labourers in the Kinabatangan region, Sabah, Malaysia, 2012–2013. Note: Immature animals because they were with their respective mothers were not recorded as a discrete encounter

Description	Ratio	Percentage
Number of encounters within 20 m of a forest border	66/99	67
Number of encounters in contiguous oil palm ≥ 5 km from any natural forest	35/99	35
Number of encounters within subsistence orchards or gardens tended by workers within their areas of residence on the estates	3/99	3
Encounters with a lone individual orangutan	80/99	81
Encounters with an adult male (flanged N = 23, unflanged N = 45)	68/99	69
Encounters with adult females with immature offspring (15 females with baby, 3 females with juvenile, 2 females with baby and adolescent)	18/99	18
Encounters of unflanged adult males or adult females without offspring (9 lone individuals, 2 × 2 equal size individuals together)	13/99	13

Table 7 Interview question series about reactions to encounters by 91 field workers in the Kinabatangan region, Sabah, Malaysia, 2012–2013. We asked questions 1–3 in sequence. We posed question 4, which is similar but not identical to question 3, at the end of the interview, following a series of questions on details about sighting location and class of orangutan(s) they encountered

Question 1—What was your reaction to the orangutan you encountered?
60% (N = 55) Neutral reaction to the orangutan • Didn't care just kept working (N = 33) • Stopped work to watch the orangutan but were not afraid (N = 22)
23% (N = 21) Negative reaction to the orangutan • Stopped work and was afraid (N = 19) • Tried to chase the orangutan (N = 2)
17% (N = 15) Elected not to answer the question • Stated they did not want to answer this question (N = 7) • Stated they preferred not to answer and were allowed to skip this question (N = 8)
Question 2—Describe the orangutan's reaction to encountering you
32% (N = 29) Neutral reaction by the orangutan • Orangutan kept quiet and watched worker (N = 21) • Orangutan just stayed eating (N = 6) • Orangutan just continued its way walking on the ground (N = 1) • Orangutan stayed hiding in oil palm tree (N = 1)
63% (N = 57) Negative reaction by the orangutan • Orangutan "ran away" through the trees or palms or if on the ground ran to a tree, climbed up and then moved away very fast through trees or palms (N = 28) • Orangutan made noise and was breaking branches (N = 24) • Orangutans was moving rapidly between trees (N = 5)
5% (N = 5) Elected not to answer the question • Stated they did not want to answer (N = 1) • Stated they preferred not to answer and were allowed to skip this question (N = 4)
Question 3—What type of problem or conflict did you have with the orangutan?
71% (N = 65) Have no problem with the orangutan
13% (N = 12) Afraid for various reasons • No fear of the orangutan. Rather they fear loss of income, because the foreman will move them away from this area but not reassign them somewhere else on this day (N = 6) • Afraid the orangutan will chase them, hurt them, or come into their house later and attack them (N = 5) • Afraid the orangutan will kidnap women, because it happened to a relative nearby (N = 1)
15.4% (N = 14) Elected not to answer
Question 4—What do you do when you have a problem with an orangutan? (N = 91)
87% (N = 79) Do nothing – **Leave animal alone.** Have no problem. Not afraid just observed the orangutan and kept working
4% (N = 4) Do nothing – **Leave animal alone,** but **so afraid they needed to stop work to watch it; Did not do anything to the orangutan**
8% (N = 7) Make noise and try to chase the orangutan. All said "people" but not necessarily the respondent themselves **throw firecrackers** at the orangutan
1% (N = 1) Report it to a manager
0% (N = 0) Elected not to answer

Discussion

This exploratory study shows that natural-forested patches in mature oil palm plantations provide stepping-stone connectivity for orangutans across the protected forest-oil palm monoculture matrix in the Kinabatangan floodplain. We found that most forest patches within estates, although degraded, contained resources of value to orangutans. Resources ranged from only a few native species trees of sufficient height for temporary shelter to a rich diversity of native tree and vine species serviceable as a longer-term refuge within the privately administered landscape. Smaller forest patch size was not necessarily an indicator of lesser value or quality since patches used by orangutans ranged from the smallest (0.5 ha) to the largest (242 ha) surveyed. Moreover, most forest islands spaced 10 km or less apart were used routinely, at least on a transitory basis, despite the fact oil palm staff rarely encounter these animals inside estates.

These results exemplify the need for a real commitment to retain preexisting "unplantable areas" (naturally forested patches) in the oil palm landscape. Although all companies involved in our study stated they intended to retain these patches, only 1 of 20 patches used by orangutans had a High Conservation Value ranking (HCV 1), meaning it was formally set aside as critical habitat for rare, threatened, and endangered species (RTE) as specified by the Round Table of Sustainable Palm Oil (RSPO). We encourage policy to improve regional stepping-stone connectivity by setting aside additional patches of land for forest restoration, especially where forest fragments are currently separated by 10 km or more. We support the RSPO recommendation to retain or restore all $\geq 25^0$ slopes rather than recontouring to terrace these areas for new planting or subsequent cycle (20–25 years) replanting. In the mineral soil landscape of the Kinabatangan region, streams and small rivers generally remain on their natural course, and many small hills and rocky outcrops remain. These natural landmarks likely help migratory males navigate across the region. Therefore, discontinuous forest patches currently appear to be sufficient to provide connectivity in this type of landscape. Conversely, plantations developed on vast flat drained peatlands, where no natural landmarks remain, may need physical corridors to retain functional connectivity between forest fragments.

In nonoil-palm planted areas, barriers to usefulness for orangutans were an absence of native species trees and vines of sufficient diversity and height necessary to provide ample cover, quantity and quality of natural food resources. However, the most pronounced negative impact on habitat quality of forest patches in estates was infestation by the invasive vine, *Mucuna bracteate*, planted in the oil palm stands. Herbicide use inside forest patches is likely not advisable. However, access roads generally ring forest patches, so if estates judiciously control *Mucuna bracteata* spread across roads adjacent to forest patches inside estates and along protected forest borders, this may be a suitable supplement to highly laborious manual cutting. Targeted enrichment planting with various native species to improve habitat within existing forest patches also is beneficial if it does not markedly intensify human disturbance.

From a synthesis of field survey data and citizen science reports from estate staff, we found females and immatures remained nearby forested areas. In contrast, male orangutans ranged widely within and between forests and in contiguous oil palm well away from any natural forest. We also found some forest patches isolated within plantations where previously unknown resident females with offspring were present decades after conversion of the surrounding forest to oil palm agriculture. These results are consistent with the community structure of orangutans, whereby males are the dispersing sex and circulate over more expansive areas between the parts of forests where related clusters of highly philopatric females with dependent offspring live (Goossens, Setchell, et al., 2006; Arora et al., 2012; van Noordwijk et al., 2012; Nietlisbach et al., 2012; Nater et al., 2013; Ashbury et al., 2020). Therefore, it appears that at least some degree of normal orangutan metapopulation dynamics necessary for long-term viability is still functioning despite drastic habitat modification in the Kinabatangan region (Ancrenaz et al., 2021; DeWoody et al., 2005; Grilli et al., 2015).

The median forest patch size used by resident females in this preliminary study was 52 ha. Another study in the Kinabatangan region reported a mean home range of 65 ha, albeit more than 45 years ago (Horr, 1975). Other published home range estimates for females of this orangutan subspecies span from 40 to 180 ha and vary with analysis metrics, habitat type, resource availability, life stage, and social dynamics (Singleton et al., 2009; Morrogh-Bernard, 2009; Wartmann et al., 2010; Ashbury et al., 2020). More study to better understand range sharing dynamics and localised feeding ecology is needed to assure the long-term survival of adult female orangutans and their dependent and semi-independent offspring in fragmented forest landscapes. This work is critical but must be conducted with great care and sensitivity, given the well-established practice of removal of orangutans found outside protected forests (Sherman et al., 2020b). The females in our study very likely survived in the forested remnants of their ancestral homes now inside oil palm plantations only because no one knew they were still there. Lifelong site fidelity, characteristic of adult female orangutans, likely predisposes this sex and dependent immatures to preferential loss during forest clearance (Ashbury et al., 2020; Marshall, Lacy, et al., 2009; van Noordwijk et al., 2012). The finding of a male skew (2.42:1) in the local sex ratio supports this supposition (Bruford et al., 2010). Moreover, these previously undetected adult females and their offspring surviving in the privately administered landscape likely represent distinct matrilines from protected forests (Goossens et al., 2005). Thus, more critically important genetic diversity may be retained in the local population than previously surmised.

The overall genetic diversity of orangutans in the Kinabatangan region remains high despite the recent anthropogenic loss of approximately 80–90% of the population (Goossens et al., 2005; Goossens et al., 2006; Goossens et al., 2006). Based on local population trends, an approximately 0.4% annual decline persists today (Table 1). Population viability analysis suggests that unnatural loss of 1% of adult females and 1–3% of dispersing males per annum would mean the population is unsustainable in the Kinabatangan region (Marshall et al., 2009). While the situation is clearly of great concern, it may not be dire if we can support the natural growth of the pre-existing local wild orangutan population, which is well-adapted to current habitat conditions and prevent unnatural losses from translocation and intentional or unintentional premature death.

This study does not diminish the importance of extensive, intact, protected forests for wildlife conservation. Instead, we show the additional value smaller forest fragments provide to support functional connectivity of orangutan metapopulations (Kadoya, 2009; Laliberté & St-Laurent, 2020). Furthermore, the extent of orangutan use of the privately administered oil palm agricultural landscape found in this study suggests that sequestering wildlife in government-protected forests alone may be insufficient for many species, including orangutans (Sales et al., 2019). Instead, integrated conservation management of the protected and privately administered agroforest matrix is required (Lele et al., 2010; Ng et al., 2021; Pascual et al., 2021). Given that the prime alluvial lowland habitat of the orangutan also is in demand for conversion to agriculture, industrial-scale farmers, as the largest private land administers in the landscape today, now have a pivotal role to play in the conservation of the wild orangutans that remain throughout their range. In addition to providing stepping-stone connectivity, tangible actions required are safe passage for male orangutans across oil palm plantations between forest patches and habitat security to assure long-term survivorship of all remaining females in situ on their ancestral land, even if this is within the privately administered landscape.

Based in part on our studies, the updated 2020 Sabah State Government Orangutan Action Plan adopted a more measured approach to translocation to facilitate improved metapopulation conservation (SWD, 2020). Nevertheless, the presumption that "agricultural best practice" requires exclusion of wildlife, and thereby any orangutan detected in or near an oil palm plantation is by definition "lost," or even "lonely," and as such requires intervention by people to "rescue" the animal and move it elsewhere, remains a firmly held dogma on the ground. In 2012, when we initiated baseline work, local oil palm plantation management perceived orangutans were "long gone" from estates 30 years after forest conversion. In 2019, based on our earlier work, plantation management was more receptive conceptually but generally remained sceptical and cautious about engaging with conservation practitioners. To overcome this reticence, judicious use of classic field science integrated with social science and citizen science techniques to facilitate interactive engagement was fundamental to building cross-sector collaborations necessary to overcome misconceptions about wild orangutan conservation in situ in the context of oil palm agriculture. (McLennan & Hill, 2012; Setchell et al., 2017; Waters et al., 2019). Furthermore, given that wild orangutans, even under normal conditions, are highly cryptic and appear even more elusive in anthropogenic circumstances, careful work by researchers with a depth of specialist knowledge of the species in these local circumstances was also crucial to the success of this work.

Overall, we found that oil palm managerial staff perceived encounters with orangutans as more problematic than labourers who encounter these animals. Interestingly, only 1 out of 91 field labourer respondents in the 2012–2013 survey said they contacted management regarding an orangutan sighting. Perhaps this reluctance to report was because the chief concern expressed by labourers was not about the animal but rather a fear of losing income if they had to stop work with no reassignment. Nevertheless, though all respondents in our initial formal interviews actively participated in descriptions of the orangutans they encountered, approximately 15% did not wish to answer any questions about attitudes, interactions, or mitigation, highlighting the need for ongoing engagement in the landscape.

A common concern at all levels of our engagement was the fear that if growers acted more positively toward orangutans, the animals would rapidly become too numerous and then become an especially challenging "pest" given the universal high regard for the species, nationally and internationally. Although a logical presumption, this misunderstanding stems from not knowing that even under idealised natural circumstances without any external threats, the maximal theoretical annual growth rate of wild orangutans is only 2% (Marshall, Lacy, et al., 2009). A related concern conveyed by estate management was the misunderstanding that conservation action for a Critically Endangered species necessitates aggressive intervention to increase animal numbers at an accelerated rate, ex situ, and reintroduce them into the landscape in large numbers to offset imminent extinction. These rational but fundamental misunderstandings are excellent examples of how complex the concepts of in situ conservation and co-existence are to grasp for the general public. They also underscore why an inclusive approach of integrated biosocial methods and sustained practical engagement that is collaborative rather than prescriptive is essential to adequately address the full range of subtleties at play in dynamic agro-forest landscapes (Campbell-Smith et al., 2012; Hill & Webber, 2010; Hockings & Humle, 2009; Hockings et al., 2015; Humle & Hill, 2016; Marsh & Chapman, 2013; McLennan & Hill, 2012).

Mixed biosocial methods can be challenging as they require a cross-disciplinary skillset and ample time to build relationships and trust across sectors (Setchell et al., 2017; Waters et al., 2019; Chazdon et al., 2020). Nevertheless, this study clarifies that without the participation of the largest land administers, who in this example happen to be oil palm growers, it would be impossible for us to support, rather than further disrupt nonhuman primate resilience in forests fragmented by agriculture. These findings apply directly to the prime alluvial lowland habitat of the orangutan and the other nine species of nonhuman primates living in the Kinabatangan region. These results are equally relevant to other riverine regions in Sabah, the rest of Borneo and Sumatra, and throughout the equatorial tropics worldwide, where little of the alluvial lowland habitat essential for many nonhuman primate species survival has escaped degradation and fragmentation from forest conversion to agriculture.

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Author Contributions FO, MA, and IL originally formulated the idea. FO and MA developed methodology. FO, HE, SP, and PS developed interviews. ARS, HS, AA, and IL facilitated contacts with companies. MDK, ARS, HS, HE, and PS conducted interviews. FO, MDK, HE, PS, and ARS conducted fieldwork. FO performed analyses. SP and PS did translations. FO and MA wrote the manuscript.

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